



History, current situation and challenges for conservation biological control

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ABSTRACT

Meeting the growing global demand for agricultural products requires the development and use of ecologically-based strategies that will allow sustainable intensification based on ecosystem services. An important component of this approach is conservation biological control. This approach encompasses a variety of management practices that protect natural enemy populations in the agro-ecosystem and enhance their fitness and ultimate impact on pests. It represents an alternative to dependence on pesticides which is associated with environmental damage and risks to human health. The interventions used to achieve conservation biological control are commonly based on managing vegetation patterns at the local scale (e.g. flowering strips that promote parasitoids by supplying nectar) or at wider scale (e.g., woodland to serve as donor habitat for natural enemies). Importantly, such vegetation management also offers scope to provide agriculture with additional ecosystem services as diverse as pollination and carbon sequestration. Despite these attractive features and the success of a small number of conservation biological control strategies, it remains underutilized. We identify as barriers to adoption the relative complexity of conservation biological control and challenges with economic evaluation, as well as perceptions and communication. Climate change is a challenge that will demand the development of flexible strategies that can respond to changes in pest distributions and/or food web structure.

1. Introduction

Increasing global demand for food requires an ecologically sustainable intensification of food production (Borel, 2017; Godfray et al., 2010; Jonsson et al., 2012; Pretty et al., 2018; Ray et al., 2012; Tilman et al., 2011). The level of growth in human activities that disrupt natural processes has raised concerns that critical biophysical systems could destabilize, triggering irreversible catastrophic changes (Rockström et al., 2009; Steffen et al., 2015). Accordingly, technologies that are based on ecological principles, such that ecosystem services are restored, are crucial to productive future agroecosystems (Bommarco et al., 2013; Matson et al., 1997; Tilman et al., 2002). An important example is conservation biological control where natural enemies are used to prevent crop losses by pests. This approach encompasses a variety of management practices that protect natural enemy

populations in the agro-ecosystem and enhance their fitness and ultimate impact on pests (Begg et al., 2017; Ehler, 1998; Eilenberg et al., 2001; Rayl et al., 2018). It represents an alternative to dependence on pesticides to maintain yields which is associated with environmental damage, risks to human health and declining availability of effective products (Barzman et al., 2015; Czaja et al., 2015). This decline in the available pesticide tools is in due to new molecules becoming increasing difficulty to find, resistance (Borel, 2017), increased regulation e.g. the EU recently banned the use of three neonicotinoids (Butler, 2018) and consumer resistance (De Vivo et al., 2016). Sustainable intensification of food production using integrated pest management (IPM) including conservation biological control, has been estimated to have reshaped farming practices on at least 20 million farms based on published accounts of education initiatives (Pretty et al., 2018) but the actual number could be much higher as this review only analyzed large

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scale initiatives. Implementing IPM practices has seen many benefits including yield increases of 5–40% with declines in pesticide use of 30–70% (Pretty et al., 2018).

2. History

The practice of conserving natural enemies or conservation biological control for pest management is not new. There have been numerous historical references to the use of natural enemies in agriculture, the most frequently mentioned natural enemies are predatory ants (Ehler, 1998; Huang and Yang, 1987) or coleopteran species (Kirby and Spence, 1826), with parasitism later recognized as an important phenomenon (Sweetman, 1958). For over 2000 years, spiders were protected by Chinese farmers through provision of temporary shelter of straw in irrigated rice field (USDA, 1982). The first recorded historical concern dated about 900 and 1200 A. D. in China where the practice of placing nests of predaceous ant *Oecophylla smaragdina* F. in mandarin citrus trees was used to manage foliar feeding insects (Sweetman, 1958). According to Kirby and Spence (1826) coccinellids were protected from birds by hop growers for aphid management in England. Pre-industrialized (and contemporary subsistence farming) systems featured practices that suppressed pest populations, yet rather than being based on scientifically tested knowledge these practices were based on experience and tradition (Abate et al., 2000; Glass and Thurston, 1978). Contrastingly, early practices to enhance natural enemy effectiveness in industrialized agricultural systems were rarely used (Ehler, 1998) and often not tested for effectiveness or practical deployment (Rabb et al., 1976; Sweetman, 1958; van den Bosch and Telford, 1964). These included planting beneficial non-crop plants in the inter-rows (Sweetman, 1958), building artificial nest sites, providing alternative food sources and the modification of management practices (van den Bosch and Telford, 1964). An early example of conservation biological control was strip harvesting of alfalfa in California, but like many early techniques it was not widely adopted due to the perceived additional cost (Ehler, 1998).

Despite the lack of interest in enhancing natural enemy efficacy, some advancements were made in the mid-1900s. For instance, it was discovered that some parasitoids need obligatory alternative hosts to persist through the year (Hardy, 1938), while other parasitoids require many species of alternative hosts when the main pest is scarce (Györfi, 1951). Furthermore, the importance of the right microclimate conditions (Taylor, 1940), olfactory responses and nectar for parasitoids had been identified (Thorpe and Caudle, 1938). Wolcott (1942) expanded on the concept that natural enemies often need additional resources to successfully reduce pest populations and this was particularly important during life stages that do not feed on the pest, such as supplying parasitoids with extra-floral resources. However, much of this work became overshadowed by pesticide-related research with pesticide selectivity or reduced use of pesticides to protect natural enemies being one of the first conservation biological control tools that became mainstream (Jaynes and Marucci, 1947; Newson and Smith, 1949; Smith and Fontenot, 1942; Yothers and Carlson, 1948).

In subsequent decades, as the concept of preserving natural enemies became accepted, research involving the use of food resources and habitat to improve natural enemy effectiveness became more common (Coppel, 1986; Landis et al., 2000). This has in part been attributed to the work by van Emden (Ehler, 1998; Landis et al., 2000; van Emden, 2002), such as van Emden (1963) showed that conservation biological could be effectively deployed in conventional agriculture, in this case by adding flowers to cabbage fields which increased parasitoid efficacy, leading to aphid pest suppression. Studies like this proved that it was not necessary to mimic naturally evolved community diversity in order to achieve enhanced biological control, instead, potentially only adding one plant species was required, making successful habitat manipulation for conservation biological control far more attainable (Way, 1966; van Emden and Williams, 1974). Following this, research explored the role

of non-crop habitat (van Emden 1965; Altieri and Whitcomb, 1979; Altieri and Letourneau, 1982) and how non-crop corridors or strips and adjacent habitat influence within-field natural enemy communities (Bedford and Usher, 1994; Coombes and Sotherton, 1986; Duelli et al., 1990; Kajak and Lukasiewicz, 1994; Thomas et al., 1991).

In the 1970s a debate started when Root (1973) challenged the thinking of the time by rejecting the ‘enemies hypothesis’ which states that natural enemies benefit more from diverse plant communities resulting in reduced pest populations compared to in monocultures. The paper proposed an alternative ‘resource concentration’ hypothesis in which herbivore pests benefit more from dense monocultures because they are easier to locate and stay because there is abundant food whereas these pests are negatively affected by more diverse plant communities due to restricted access and reduced abundance of host plants (Root, 1973). The debate of when one or both of these hypotheses have occurred was an important step in the development of conservation biological control as it made researchers’ question how habitat manipulation was affecting the higher trophic levels and what were the main drivers of observed pest suppression or lack of (Andow and Risch, 1985; Gurr et al., 1998). In the research that followed, it was recognized that habitat manipulation which benefits the third trophic level (natural enemies) may also benefit the second trophic level (pests) (Price et al., 1980; Collins and Johnson, 1985; Gurr et al., 1998). Furthermore, the fourth trophic level (hyperparasitoids and predators of beneficial natural enemies) may reduce biological control efficacy and this effect could be enhanced by habitat manipulation (Stephens et al., 1998). Other major steps forward for conservation biological control during the late 20th century included understanding the crucial role of floral morphology and plant chemistry in the ranking of plants for habitat manipulation (Baggen and Gurr, 1998; Gurr et al., 1998). A major realization was that habitat manipulation can have multiple benefits and therefore have added value of which conservation biological control can be part of (see Section 4.2), for instance providing nesting sites and food for vertebrates of conservation value (Aebischer and Blake 1994; Bence et al., 1999; Thomas et al., 2001). This led to wider adoption of habitat manipulation with some governments adopting policies to encourage habitat manipulation in agriculture through schemes such as those in the United Kingdom (Lobley and Potter, 1998; Ovenden et al., 1998). Motivated in part by the development of resistance to the new generation of selective pesticides, the turn of the century has marked a new era of growth in conservation biological control research (Barbosa, 1998; González-Chang et al., 2016; Gurr et al., 2018; Gurr et al., 2017; Jonsson et al., 2008; Pickett and Bugg, 1998).

3. Current situation

Contemporary conservation biological control strategies are often supported with empirical research in contrast to earlier, well-intentioned but simplistic notions that any form of plant diversity would prove beneficial (Begg et al., 2017; Cullen et al., 2008; Fiedler et al., 2008; Gurr and You, 2016; Jonsson et al., 2008; Khan et al., 2008; Landis et al., 2000; Wyckhuys et al., 2013). Practices are underpinned by knowledge of pest and natural enemy ecology and, in more recent research, interactions with field, farm and landscapes (Begg et al., 2017; Jonsson et al., 2008).

The use of flowering plants to enhance the effectiveness of natural enemies has been widely investigated (Gurr et al., 2017) and implemented in numerous systems such as: blueberry (Blaauw and Isaacs, 2015), lettuce (Brennan, 2016), potatoes (Tschumi et al., 2016), soybean (Woltz et al., 2012) and rice (Zhu et al., 2018). In recent years a former focus on specific insect-plant interactions has begun to shift to adoption of a trait-specific approach so that more generalizable rules might be formulated rather than having to screen multiple candidate plants for each new enemy-pest-crop system (Campbell et al., 2012; Gamez-Virues et al., 2015; Perović et al., 2018; van Rijn and Wäckers,

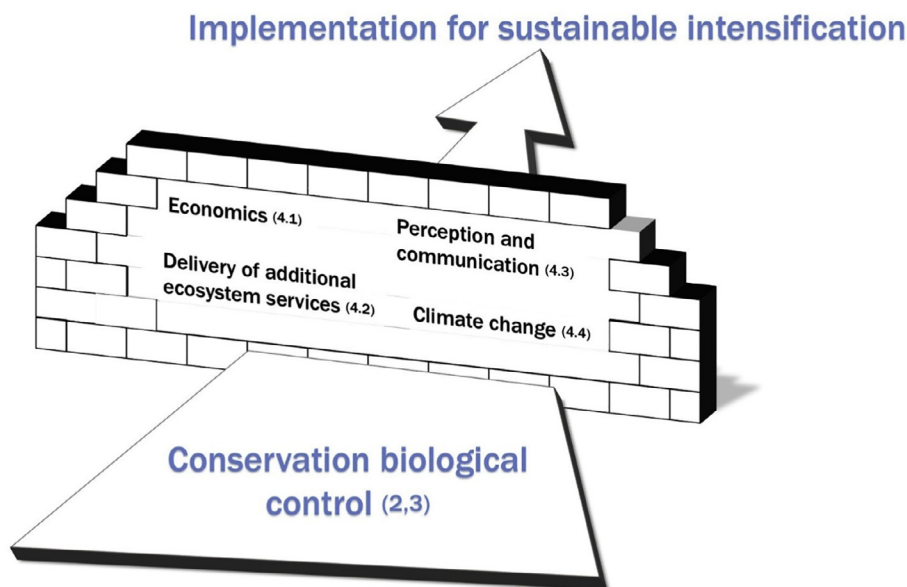


Fig. 1. Conceptual diagram of the barriers to implementation of conservation biological control. (Parenthetical numbers indicate the relevant sections of body text).

2016). Research into plant species has also moved away from the use of exotic and naturalized plant species towards use of local or native species that are often better suited to local conditions and that present a smaller risk of becoming invasive weeds (Fiedler and Landis, 2007; Gonzalez et al., 2016; Pandey et al., 2018; Shields et al., 2016).

A large sub-discipline within conservation biological control is the study of landscape scale effects of non-crop vegetation, their complexity, spatial arrangement and connectivity (Begg et al., 2017; Chaplin-Kramer et al., 2011; Schmidt and Tscharntke, 2005; Thies et al., 2005; Thies et al., 2003; Tscharntke et al., 2005). Non-crop habitat in the landscape is a potentially important, but inconsistent contributor to improved pest management (Karp et al., 2018; Tscharntke et al., 2016). For instance, when the wrong plants are deployed for the intended natural enemies, conservation biological control is not enhanced (Irvin et al., 2006). Local management decisions such as pesticide use patterns and availability of nectar and pollen rewards also drive ultimate natural enemy impact (Tscharntke et al., 2016; Zhang and Swinton, 2009).

4. Challenges

4.1. Economics and uptake of conservation biological control

Consumer attitudes towards agriculture are changing and public mistrust in intensive agricultural systems has become more common (Kleijn and Sutherland, 2003; Pretty and Bharucha, 2014; Struik and Kuyper, 2017; De Vivo et al., 2016). Agricultural intensification has well known costs, due to the degradation or loss of numerous ecosystem services resulting in increasing rates of topsoil compaction, water quality loss, methane emissions from livestock, reduced pollination and pest control capacity (Pretty et al., 2000; Tait and Cullen, 2006; Lichtenberg et al., 2017; Tegtmeier and Duffy 2004). IPM and conservation biological control are well-placed to help mitigate the negative aspects of intensive agriculture by reducing the use of synthetic inputs, particularly insecticides (Gurr et al., 2016), lowering the health risks to agricultural workers and consumers as well as increasing other ecosystem services such as pollination (Fiedler et al., 2008; Wyckhuys et al., 2013).

Although there are sometimes conflicting results, there is mounting evidence that farm management practices and increased plant diversity across landscapes can improve arthropod biodiversity (Lichtenberg

et al., 2017) potentially leading to improved pest suppression (Tscharntke et al., 2016; Muneret et al., 2018). However, caution must be taken as non-crop areas surrounding fields have inconsistent effects on crop pests and predators and often does not enhance biological control (Karp et al., 2018). Despite the potential advantages of conservation biological control, and the wider need for ecologically-based approaches that can allow sustainable intensification, its actual implementation remains limited. Begg et al. (2017) conclude that the greatest limitation to the development of effective conservation biological control is the inability of natural enemies ... “to deliver effective, reliable and robust biological control of pests”.

Several studies have noted the gap between the contribution that biological control in general could and does make, seek explanations for the deficit, and offer prescriptions on how to promote increased use (Barratt et al., 2018; Begg et al., 2017; Cullen et al., 2008; Naranjo et al., 2015; Tscharntke et al., 2016). Tscharntke et al. (2016; 449) identify five cases where natural habitat may fail to support conservation biological control, where ... “(1) pest populations have no effective natural enemies in the region (2) natural habitat is a greater source of pests than of natural enemies (3) crops provide more resources for natural enemies than does natural habitat (4) natural habitat is insufficient in amount, proximity, composition or configuration to provide large enough enemy populations needed for pest control, and (5) agricultural practices counteract enemy establishment and biocontrol provided by natural habitat.” In summary, several factors can influence the relative importance of natural habitat for biocontrol, and those factors need to be considered when designing measures to restore or maintain natural habitat to enhance biocontrol.

Farmers who operate in highly competitive industries are often risk averse decision makers and favor systems that deliver high yields with low risk (Tracey, 2014). Local-scale conservation biological control has not been viewed favorably in many systems as it can be knowledge-dependant and, potentially, labor intensive (see Section 4.3). Regional scale conservation biological control has additional barriers of coordination or collaboration across multiple landholders (Geertsema et al., 2016) where individual farmers can question how much their crops will benefit in proportion to their perceived effort and expense.

Conservation biological control at local or regional scale is more likely to be widely adopted if there is clear-cut evidence that it makes a positive economic contribution (Fig. 1). Sadly, such evidence is only rarely available and studies that extend to considering economic

benefits such as Gurr et al. (2016) are in the minority. Onstad and Knolhoff (2009) determined from a survey of economic entomology literature that less than 1% of research papers report economic evaluations of pest management tactics. Naranjo et al. (2015) summarize 17 studies in 10 different countries, but observe that after more than fifty years of IPM, it is still a struggle to identify the value of conservation biological control.

There are several explanations for this difficulty. Some economic evaluations have used economic threshold analyses that are static, partial equilibrium, and often do not capture all the impacts of conservation biological control. Comprehensive economic evaluation of conservation biological control requires measurement of a range of input costs and assessment of the diverse benefits. Whereas some benefits are private goods with market prices, others have public good aspects and lack market prices. A range of methods are needed including non-market valuation (Hanley et al., 2015). While pest and natural enemy thresholds are easy to interpret and in IPM, force end-users to recognize the role of natural enemies in pest management decisions, in practice they are difficult to calculate and do not exist for many crops (Giles et al., 2017; Ramsden et al., 2017). Rigorous evaluation of the impact of conservation biological control requires careful experimental design to ensure potentially confounding factors are controlled and that economic benefits can be isolated and assessed.

Careful experimental design requires collaboration between farmers, farm advisers, agronomists, entomologists, economists and econometricians. Because collaboration takes time and is costly, a determined effort is needed to ensure success. Numerous calls have been made for agri-environmental research to exit research ‘silos’ (Loreau, 2010; Mace et al., 2012; Struik and Kuyper, 2017) but such approaches are still rare in the scientific literature (McDonough et al., 2017; Struik and Kuyper, 2017). Naranjo et al. (2015) observes that funding sources increasingly seek pre-planned evaluations and hence there is incentive for biological, social and economic researchers to work in multidisciplinary ways to develop and execute robust evaluations of conservation biological control. Barratt et al. (2018) recommend that biocontrol practitioners, economists, social scientists and stakeholders collaborate early to ensure the needed data (social, economic, environmental) are collected to facilitate evaluation.

There is also reluctance to collaborate and develop multidisciplinary research in other fields including biodiversity projects. Cullen and White (2013) comment that for species conservation evaluation to have an impact on species conservation, it needs to be adopted by practitioners and policy-makers, and has to be seen as an integral and core part of conservation rather than as an add-on, advice that seems pertinent as well for conservation biological control.

4.2. Multiple ecosystem services

As noted in the previous section, conservation biological control can have multiple benefits that complicate economic evaluation, and these effects can extend beyond pest management into other ecosystem services. Because conservation biological control can enhance elements of the arthropod community and its functions already present in a given agroecosystem, several ecosystem services can be enhanced in addition to pest suppression. These include pollination, nutrient cycling, soil moisture retention, weed control, aesthetics and human well-being (Wratten et al., 2012).

Clearly, if a vegetation management intervention offers scope to enhance multiple ecosystem services – rather than conservation biological control alone – this potentially will make the effort and cost of the intervention easier to justify and more attractive to farmers and policy makers. On the other hand, the ecological and practical knowledge required to realize the potential benefits and avoid negative trade-offs is in its infancy. In addition, quantifying ecosystem services can be difficult as their benefits may extend beyond individual farms (Wratten et al., 2012) and some services such as aesthetics and human well-being

do not have monetary value but can contribute to improving mental health (Roberts et al., 2015). These factors constitute significant barriers to adoption (Fig. 1).

Because the scientific disciplines associated with multiple ecosystem services are not restricted to the biological control or biodiversity domain, a multidisciplinary approach is needed in order to fully understand these interactions (Mace et al., 2012; McDonough et al., 2017; Struik and Kuyper, 2017). The field of ecosystem services research has been growing rapidly since this concept was globally quantified in natural ecosystems for the first time in 1997 (Costanza et al., 1997; Daily, 1997). Research activity in this multidisciplinary area is increasing rapidly and revealing how consequences of manipulating agricultural systems to enhance such functionality may not always be straightforward. For example, it is well known that adding floral resources to agroecosystems to enhance pollination and biological control agent efficacy may not deliver expected results (Wratten et al., 2012). Other examples of attempts to generate multiple ecosystem services, including the deployment of bioenergy crops in complex landscapes (i.e. not as monocultures) can depend on the bioenergy crop type, its arrangement in the landscape and which other plant species are present (Werling et al., 2014). Littlejohn et al. (2015), have identified at least 15 ecosystem services associated with plantings of the sterile hybrid biofuel feedstock grass, *Miscanthus* × *giganteus* Greef and Deuter. These services include improved pasture growth and habitat for vertebrates and invertebrates. Sometimes, however, ecosystem provision in agriculture, although intuitive, is more complex than envisioned. A key case is that hedgerows can act as winter refugia for beneficial arthropods. While this is generally true, there may be no ecosystem service delivery (i.e. biological control of pests) within the crop if the arthropods remain in the refuge all year (e.g., McLachlan and Wratten, 2003). There are other reasons why such refugia do not deliver ‘expected’ biological control advantages (see Section 4.1) (Karp et al., 2018; Perović et al., 2018; Tschamtkke et al., 2016). Opposite results can arise when only one ecosystem service is ‘targeted’ but unintended multiple ecosystem services occur. The case of ‘beetle banks’ as refugia for beneficial arthropods in European cereals is a good example (see Section 4.3). Additional ecosystem services have arisen, unrelated to the initial aim of contribution to cereal-aphid management. These benefits include provision of habitat to voles (*Microtus arvalis* Pallas) as prey for the barn owl (*Tyto alba* Scopoli). These voles can be agricultural pests in Europe so it follows that the deployment of beetle banks has led to farmland tri-trophic level interactions beyond invertebrate pest management (Jacob et al., 2014).

However, multidisciplinary research in this area has been rare, accounting for only 1% in a recent review (McDonough et al., 2017). Varied social, cultural and institutional factors could be affecting this rarity of multidisciplinary efforts by scientists, and one barrier is specialized terminology used for communicating insights between disciplines (Hesketh and Sayir, 2018; McDonough et al., 2017). Barriers to effective cross-disciplinary work include worldviews and terminology unique to individual disciplines (Costanza and Kubiszewski, 2012). A simple example of language differences across disciplines is the word “community” which has different meanings to an ecologist and a sociologist. Therefore, a consensus in terminologies and methodologies that promotes interdisciplinary communication is needed to solve these complex ecological problems (McDonough et al., 2017; Struik and Kuyper, 2017).

It seems undeniable that conservation biological control would benefit from a more multidisciplinary approach, in which ecological, socio-cultural, agronomic, economic and political forces interact more effectively (Altieri and Toledo, 2011; Reganold and Wachter, 2016; Struik and Kuyper, 2017; Michaud, 2018). Agricultural intensification based on increased use of inputs has well known costs environmentally and economically, and it is urgent to develop a sustainable agricultural intensification approach that considers biodiversity as a key component to restore missing ecosystem services.

As the science of ecosystem services has advanced to include multiple ecosystem services, there has been an increasing awareness that simply adding one ecosystem provider may lead to unexpected ecosystem dis-services. For example, adding a flowering plant to provide SNAP (shelter, nectar, alternative prey, pollen) to beneficial insects may lead to that plant becoming a weed (Gurr et al., 2017). Also herbivorous pests may feed on it or its nectar and pollen which may improve pest fitness. The latter may not be a harmful consequence if the fitness of the targeted beneficial insect is enhanced to a greater extent (Irvin et al., 2006). The consequences of this type of effect were investigated by the modelling approach by Kean et al. (2003) can help explore the relative importance of such effects. Such added plants may compete with the crop for water or nutrients leading to increased frost risk. Trophic levels higher than the second or third may also be unexpectedly involved. For example hyperparasitoid wasps attacking beneficial parasitoids may also benefit from floral resources, potentially limiting the pest population reduction effects of the added flowers. This was referred to by Varennes et al. (2014), using molecular analyses of aphid mummies. The aphid hyperparasitoid *Asaphes vulgaris* Walker (Pteromalidae) was found using these methods in mummies of the cabbage aphid *Brevicoryne brassicae* L. Although trophic-level interactions were not explored in this work, Araj et al. (2009, 2011) showed that hyperparasitoids such as *Dendrocerus aphidum* Rondani did benefit from access to nectar of buckwheat, *Fagopyrum esculentum* Moench. This insect antennated its host and spent more time searching than when fed with water only. An example of where potential ecosystem dis-services of this type need to be managed is the invasion of commercial glasshouses in the UK by an aphid hyperparasitoid which attacks parasitoid biological control agents (Jacobson, 2011). The recognition and quantification of ecosystem dis-services as a result of biodiversity-led interventions in agriculture is still in its infancy and enhanced research activity in this area is urgently needed. The development of ecosystem service enhancement delivery systems and pathways to implementation will be limited, and end-users' trust in them damaged, if such negative interactions are discoveries only after ecosystem enhancement protocols are deployed commercially. Further discussion of ecosystem dis-services can be found in the review by Gillespie and Wratten (2017).

4.3. Communication and perceptual barriers to research and adoption

Public attitudes towards agriculture are shaping farming practices by changing end-users' views and legislation. (Kleijn and Sutherland, 2003; Reganold and Wachter, 2016). This has its roots in the work of Rachel Carson's "Silent Spring" (Carson, 1962), where the negative impacts of non-selective pesticides were first widely publicized. Despite the well-known effects of non-selective pesticides on the natural enemy community (Palumbi, 2001), new advances in the production of selective pesticides can help the uptake of conservation biological control strategies, as some pests in highly intensified agricultural landscapes are difficult to control by chemical or biological control alone (Torres and Bueno, 2018). Selective pesticides offer an interesting opportunity for farmers that would like to shift from monoculture-based agricultural systems into diverse and sustainable ones, as the multiple ecosystem services provided by these natural enemies are not negatively affected by the application of selective insecticides that aim at a particular pest species (Torres and Bueno, 2018). Also in recent years, a huge advance in genetically modified crops has occurred, where crops expressing toxins from *Bacillus thuringiensis* (Bt crops) have been proposed as part of integrated pest management strategies (Tian et al., 2015). This proposal has its foundations in the fact that so far there are no studies showing significant effects of Bt crops on the natural enemy community at field level (Comas et al., 2014; Guo et al., 2016; Naranjo, 2005), which highlights their potential for being included as part of a conservation biological control strategy. Thus, considering that biological control is a well recognised component of an integrated pest management approach, the use of selective pesticides and genetically modified

crops could improve the adoption of conservation biological control strategies during the transition towards agro-ecological systems, especially in monoculture-based agroecosystems that are heavily subsidised by chemical inputs. However, mistrust on conventional farming practices for pest control has not only concerned the public or scientists working on food production, but also extended to biological control of pests, reflecting the non-target effects of some agents introduced in classical biological control programs in the last century (Brodeur et al., 2018; Howarth, 1991).

Considering that the funding of biological control programs has largely depended on public institutions, a negative public image of this discipline can adversely affect funding, mainly because politicians are sensitive to public awareness and perceptions (Barratt et al., 2018; Brodeur et al., 2018). A clear advantage, however, in contrast with classical biological control is that conservation biological control has less risk by enhancing all-ready existing natural enemies in the local area. Furthermore, individual farmers can implement conservation biological control without the need for government funding.

Despite the foregoing challenges, biological control remains an essential tool for pest control, especially in organic and subsistence agricultural systems that do not rely on synthetic pesticides. Research on classical and augmentative biological control has also increased through time, with increasing international collaboration between scientists (Brodeur et al., 2018). With new tools to understand trophic relationships between arthropods in agricultural systems, such as molecular gut content analysis and next generation sequencing, research on conservation biological control has also increased (González-Chang et al., 2016; Gurr et al., 2018). Although scientists are generating new knowledge, there is a growing gap between this body of knowledge and implementation, largely because collaboration with end users is often inadequate (Wyckhuys et al., 2018). However, efforts have been made to increase communication between scientists and farmers through the use of participatory methodologies such as 'farmer field schools' (Amudavi et al., 2009) and 'farmer to farmer' strategies (Altieri and Toledo, 2011; Holt-Giménez, 2008). The integration of appropriate extension methodology with research is crucial implementing sustainable practices, and the success of the approaches mentioned above has been related to trust and common language used by farmers who teach other farmers (Holt-Giménez, 2008). Farmers will test a particular novel technology on their farms to evaluate its suitability leading to neighbouring farm also testing and eventually adopting such technology (Amudavi et al., 2009). Usually, farmer teachers or innovators combine their in-field experience with scientific knowledge, so the communication between these teachers and scientists must be fluid and smooth; both parts need to talk a similar language (Holt-Giménez, 2008; Altieri and Toledo, 2011). Advances in ecological knowledge need to be drawn together in a format that is easily accessed, deployed and understood by the end user, which might include videos, leaflets, webpages, postcards, or even the social media (Wyckhuys et al., 2018). Where available, the use of smartphones, tablets and computers can boost the use of knowledge by farmers (Barratt et al., 2018; Wyckhuys et al., 2018). Speaking a different language between scientists and farmers is not only a potential barrier for adopting conservation biological control in farms (Fig. 1), but also for other stakeholders, such as policy makers, business managers and public administrators that can help in promoting more diversified agroecosystems. Scientists need to take into account regional and cultural differences, such as language, cultural traditions and the desire of farmers for quick economic returns (Barratt et al., 2018).

A promising strategy to increase the uptake of conservation biological control are locally-based 'recipes' for pest control using functional biodiversity that farmers can easily adopt (Gurr et al., 2017). There is an urgent need for practical advice on how to translate these conservation biological control concepts into action. An example of a service providing protocol is European 'beetle banks' developed by the University of Southampton and the Game and Wildlife Trust, UK

(Thomas et al., 1991; Thomas et al., 1992). These banks are ‘ecological islands’ within agroecosystems on which predatory beetles and other biological control agents spend the winter. In the spring, they emigrate from the banks into the field and contribute to the biological control of aphids and other pests (Collins et al., 2002). These islands can also act as refuges for rare farmland mammals (Bence et al., 1999), game birds (Aebischer and Blake 1994; Thomas et al., 2001) and have become hunting territory for predatory birds such as owls (Jacob et al., 2014). A clear service providing protocol exists for establishing these banks (<https://www.gwct.org.uk/farming/advice/sustainable-farming/beetle-banks/>). They are widely used in Europe, currently more for vertebrate conservation than for biological control and have recently been adopted as part of the agricultural policy of the Netherlands (Torrance and Parish, 2018). Service providing protocols have also been developed for managing the rice leafhopper *Nilaparvata lugens* Stål for Southeast Asia (Gurr et al., 2016). Protocols of this nature are novel in concept and still rare due to the variation in ecological and climatic conditions worldwide (Gurr et al., 2017).

Despite sometimes conflicting results (Karp et al., 2018; Tschamtkte et al., 2016), there is mounting evidence that local farm management practices and plant diversity across landscapes can be manipulated to improve arthropod biodiversity (Gurr et al., 2016; Letourneau et al., 2011; Lichtenberg et al., 2017). An important caveat is that landscapes with more native vegetation do not automatically lead to fewer crop pests in isolation of appropriate local management (Karp et al., 2018). Clearly there is still work to be done linking spatial scale effects to other disciplines of ecology (Mace et al., 2012), agriculture (Struik and Kuyper, 2017) and social sciences (Barratt et al., 2018). These linkages are key to achieving a truly multidisciplinary understanding and realizing the full potential of conservation biological control and more widely, sustainable intensification.

4.4. Climate change and conservation biological control

Climate change is a major global challenge for humanity and much has been written on this phenomenon and possible mitigation approaches. Here we focus on its probable effects on conservation biological control: (i) the direct effects of increasing temperatures and climate variability and (ii) indirect effects through the disruption of species interactions across trophic levels in populations and food-web dynamics. Research will need to remain current with climate-facilitated changes in the direct and indirect interactions of natural enemies and pests to ensure that conservation biological control systems remain resilient to changes (Fig. 1). The social impacts of climate change including human population and cropping pattern shifts will also affect conservation biological control strategies (Wilson et al., 2018) but this is not discussed here.

4.4.1. Phenology

Changes in temperature, precipitation and other climate factors will alter the phenology of both pests and natural enemies (Castex et al., 2018; Forrest, 2016; Laws, 2017; Rafferty et al., 2013). Development time will generally decrease with increasing temperatures, potentially resulting in altered diapause patterns and more generations per year (Laws, 2017; McVean et al., 1999; Thomson et al., 2010; Tobin et al., 2008; Trnka et al., 2007). Different developmental stages of natural enemies and pests can occupy separate microhabitats and have different thermal tolerances. Therefore, climate change may benefit some developmental stages such as adults but occasionally prevent juvenile stages from reaching maturity (Kingsolver et al., 2011). As discussed by Van Dyck et al. (2015), climate change may provide environmental cues that trigger natural enemies and prey to take poor developmental pathways, leading to developmental traps and lost generations. Where additional incomplete generations occur, with little or no recruitment will result. This can be disastrous for some species as illustrated by the wall brown butterfly, *Lasiommata megera* L., in north-west Europe. In

areas of local extinction, this species had developed a partial third generation without larval diapause at the end of summer whereas in existing populations only 42.5% do so, allowing those populations to persist (Van Dyck et al., 2015). In addition to developmental traps solely related to climate, the potential decoupling of natural enemy and pest phenologies could be catastrophic for biological control (Thomson et al., 2010; Welch and Harwood, 2014). Early in the season there may be no pests available in suitable stages when natural enemies become active (Grabenweger et al., 2007), potentially resulting in high mortality in the third trophic level. In contrast, a late arrival of natural enemies could also be disastrous (Thomson et al., 2010). Modelling approaches can be used to compare potential synchronization in a changing climate (Castex et al., 2018; Thomson et al., 2010). This has been feasible only in relatively simple systems which involve a single natural enemy, pest and sometimes host plant (Castex et al., 2018; Furlong and Zalucki, 2017; Hoover and Newman, 2004; Musolin, 2007). However, successful biological control systems often involve a complex community of different guilds of natural enemies that may differ between host plants, seasons and regions (Cardinale et al., 2006; Tschamtkte et al., 2007). For instance, in Australia, the moth pest *Epiphyas postvittana* Walker has up to 25 parasitoid species contributing to its biological control (Paull and Austin, 2006). Many natural enemies will have complex interactions between each other, prey and host plants (González-Chang et al., 2016; Perović et al., 2018). These synergistic, additive and antagonistic interactions in key biological control food webs need to be modelled in conjunction with climate data to anticipate how climate change will affect biological control outcomes (Tylianakis and Binzer, 2014).

4.4.2. Interspecific interactions

Changes in atmospheric gas composition and other climate factors can have profound effects on natural enemy and pest interactions, and are often mediated by host plants (Laws, 2017). Climate change can alter plant growth, nutrients composition (Zvereva and Kozlov, 2006) and secondary metabolites (Ode et al., 2014). These modifications may change pest feeding behavior and nutrient content which in turn affect natural enemy searching efficiency and recognition of the pest (Boullis et al., 2015; Laws, 2017; Hosseini et al., 2018). The production of plant volatile organic compounds (VOCs) is generally enhanced by higher temperatures but can be affected positively or negatively by increased CO₂ levels (Peñuelas and Staudt, 2010). VOCs are used by pests to locate suitable host plants, and by natural enemies to find prey or hosts (Laws, 2017; Van der Putten et al., 2010). It is currently unclear how conservation biological control will be affected by changes in VOC production resulting from climate change. Increased CO₂ levels may lead to increased damage by chewing pests through suppressed plant defences mediated by the jasmonic acid pathway. However, increased CO₂ may also lead to enhanced plant defenses against phloem feeding pests which use the salicylic acid pathway (Ode et al., 2014). Natural enemy and pest chemical signalling may also be directly affected by increased temperature. For instance, semiochemical production of ladybeetle larvae can be enhanced with increased temperatures, resulting in reduced oviposition by nearby female conspecifics (Sentis et al., 2015). Natural enemy consumptive effects will probably vary with climate change as increased metabolism may not increase predation rates if body mass, predator or prey nutrient content are modified (Gao et al., 2010; Laws, 2017). For example, lacewings developing under high CO₂ conditions had a lower predation rate than those that developed under ambient conditions, probably because under high CO₂ conditions their aphid prey had less available protein (Gao et al., 2010). Modified climates can mediate natural enemy non-consumptive effects via temperature effects on natural enemy and pest nutrient stoichiometry and metabolic rates (Laws, 2017; Schmitz et al., 2016). Temperature increases can increase pest requirements for carbohydrates for predator evasion (Hawlena and Schmitz, 2010) to compensate for increased metabolic rates (Chown and Nicolson, 2004) and increase

protein requirements for higher growth rates (Elser et al., 1996). The expected reduced plant quality may require pests to feed more resulting in reduced predator escape responses such as with aphids (Hentley et al., 2014). However, climate change may alter the preferred microhabitats of natural enemies due to the fact that they have generally lower thermal tolerances than their prey; pests could then exploit these effects to reduce the risk of predation. This effects has been observed in grasshoppers when avoiding predation by spiders (Barton, 2010; Barton et al., 2009). Furthermore, changing microhabitat preferences and pest nutrient stoichiometry may stimulate prey switching by natural enemies, resulting in a loss of control (Desneux and O'Neil, 2008; Prasad and Snyder, 2006). While it is difficult to make generalize how climate change will affect interspecific interactions these factors will be pivotal in maintaining or improving conservation biological control.

4.4.3. Pest and natural enemy distribution changes

Climate change may create novel and possibly depauperate communities with novel biological control dynamics, including range expansions and host shifts that might not be synchronized between natural enemies, pests and host plants (Castex et al., 2018; Lamichhane et al., 2015; Laws, 2017). Many pests are expected to have range expansions as they track crops and other host plants to newly favorable areas (Laws, 2017; Musolin, 2007; Trnka et al., 2007), particularly those that are cold-limited (McDonald et al., 2000; Sutherst et al., 2007; Thomson et al., 2010). For instance, pine beetles which devastate forests in eastern United States are predicted to expand northwards with increased minimum winter temperatures (Trân et al., 2007). Another example is the pink bollworm, *Pectinophora gossypiella* Saunders, which will be able to invade cotton crops in areas from which it was previously excluded due to severe frosts (Gutierrez et al., 2008). In addition to range expansions there may also be range constrictions by pests that require cooler and wetter climates (Hoffmann et al., 2008). Although climate change is expected to have a predominantly positive effect on pests, it is more difficult to estimate how climate change will affect natural enemies. For instance, some natural enemies will be excluded or have low biological control efficacy within regions in their current range where temperatures exceed their optimal or critical maxima that their pest prey could exploit (Castex et al., 2018; Furlong and Zalucki, 2017; Thurman et al., 2017). In Australia, it is predicted that by 2070 *Diadegma semiclausum* Hellen will only benefit more than its host, *Plutella xylostella* L., in the very southern parts of Australia such as Tasmania (Furlong and Zalucki, 2017). Additionally, it is pests invading new areas that may have lower parasitism rates because they lack native specialist parasitoids (Cornell and Hawkins, 1993; Thomson et al., 2010). Furthermore, a meta-analysis by Stireman et al. (2005) suggested that hymenopteran parasitism of larvae will decline with increasing climatic variability. It is concerning that hymenopteran parasitoids are generally expected to perform poorly in future climates as they relied on as dominant insect biological control agents (Stiling and Cornelissen, 2005). Whereas there is some literature on climate change-driven parasitoid distribution changes in a biological control context, particularly host-specific species, there is little literature available for generalist natural enemies. This might be because groups such as beetles and spiders are often considered less effective individually than host-specific species.

4.4.4. Maintaining conservation biological control in a climate change scenario

Climate change is predicted by many to increase pest outbreaks and disrupt biological control (Castex et al., 2018; Diehl et al., 2013; Thomson et al., 2010; Thurman et al., 2017). It is unlikely that releasing classical or augmentative biological control programs will keep pace with the many new pest outbreaks and new invasions predicted (Dukes and Mooney, 1999; Thurman et al., 2017). Therefore, reliance on conservation biological control may increase and local natural enemies will need to adapt to prey on invasive pests (Schonrogge et al., 2012).

This suggests that generalist natural enemies should be investigated in novel environments where pests are predicted to expand. These are likely to have greater resistance to climate change and adapt better to novel communities and phenology mismatches compared to specialists (Thurman et al., 2017). Generalist natural enemies have alternative prey sources when the pest is absent (Stiling and Cornelissen, 2005) and can occupy multiple microhabitats (Cisneros and Rosenheim, 1998; Schmitz and Barton, 2014) which may be particularly important during range expansions and shifts into novel communities (Thurman et al., 2017). Furthermore, natural enemy genetic and community diversity needs to be conserved to allow adaptation to changing climates (Hoffmann et al., 2017; Jonsson et al., 2017). Natural enemies in different orders and guilds generally have varied tolerances and responses to changes in climate (Guzmán et al., 2016; Harmon et al., 2009). Because different orders and guilds of natural enemies will vary in their tolerance and responses to changes in climate (Guzmán et al., 2016; Harmon et al., 2009), a diverse natural enemy community can be a reservoir of future biological control agents (Jonsson et al., 2017). Increasing natural enemy diversity may also enlarge the temporal window for pest suppression (Thurman et al., 2017). Predicting tri-trophic interactions within diverse natural enemy food webs may also be essential for understanding climate change impacts on conservation biological control (Castex et al., 2018; Thomson et al., 2010; Thurman et al., 2017). This could be achieved by comparing models of climate and phenology and using sensitivity analysis to represent future climates (Castex et al., 2018; Gilioli et al., 2016; Hirschi et al., 2012; Northfield et al., 2017). Furthermore, modeling could be used to match plant species that are known to provide SNAP (shelter, nectar, alternative prey, pollen) for natural enemies to suitable future climates (Gurr et al., 2017). Suitable plants for habitat manipulation in future climates are currently unknown and direct laboratory and field research is required to find potential candidates. Non-crop vegetation will be crucial in maintaining biological control efficacy during climate change by maintaining relatively diverse natural enemy communities in agroecosystems and providing natural enemies with a buffer against weather extremes (Thomson et al., 2010).

5. Conclusion and prospects

Despite empirical evidence that conservation biological control can be an effective means of reversing the negative effects of agricultural intensification, consideration of natural enemies in pest management is inconsistent across cropping systems and pesticide resistance remains a worldwide problem (Begg et al., 2017; Borel, 2017; Wilson et al., 2018; Zhang and Swinton, 2009). The history of conservation biological control documents many techniques and interventions, but their potential has remained unrealized as a result of economic, perceptual and communication barriers (Fig. 1). These are key factors that have limited the integration of conservation biological control into existing farming practices (Ehler, 1998). Additional factors include government policies and the influence of agro-chemical companies (Rayl et al., 2018; Reganold and Wachter, 2016; Michaud, 2018). Set against these barriers to adoption, concerns about pesticide residues in food and loss of biodiversity have resulted in the removal of several pesticides and a tightening of registration processes for newer products, especially in the European Union (Czaja et al., 2015). Consumer influence has combined with these factors to encourage the uptake of IPM as a means of reducing reliance on synthetic insecticides. A risk-adverse regulatory environment for chemical pesticides now extended to biological pesticides (e.g., microbial and plant extract-based products) and diminishes opportunities to substitute biological for chemical pesticides (Czaja et al., 2015). This risk adverse environment also affects potential to classical biological control programs (Brodeur et al., 2018). However, this constitutes an opportunity for conservation biological control which avoids regulatory hurdles by using locally present natural enemies and potentially allows end users to develop and implement

ecologically based solutions to their local pest problems.

A further potential driver for the adoption of conservation biological control is that consumers and policy makers in some jurisdictions have been prepared to pay higher prices for products from systems in which less pesticides are used, and make payments to landholders for stewardship and other agri-environmental schemes in which biodiversity is enhanced and protected. Whilst these are positive effects, agri-environmental schemes have lacked robust evaluations (Kleijn and Sutherland, 2003; Naranjo et al., 2015). Looking ahead, policy makers and end users need to be better able to assess the effects of interventions on multiple ecosystem services. These extend beyond conservation biological control to some that relate directly to agriculture (e.g., pollination and nutrient cycling) and to others of wider importance including biodiversity protection and carbon storage. A key connection here is that if vegetation management interventions can help mitigate the effects of climate change, the adverse effects of this global phenomenon on conservation biological control and agriculture more generally can be reduced. In order to promote the use of conservation biological control in sustainable agricultural systems, the above-mentioned benefits of this pest management strategy on the provision of several ecosystem services needs to be communicated outside the scientific community to the public, farmers and policy makers in such a way that is easily understood by them.

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